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ORIGINAL PAPER

Spatial analysis and structure of a cross-timber stand in the TallGrass Prairie Preserve (Pawhuska, Oklahoma)

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Abstract: I analyzed the spatial distribution and structure of trees in a cross timber forest in the Tallgrass Prairie Preserve (Pawhuska, Oklahoma, USA). I mapped and measured diameter of all stems, saplings (>1.5 m tall) and dead trees in a 4-ha plot. The stand was dominated by *Quercus stellata* and *Q. marilandica*. In total, I mapped 7,636 trees, consisting of 6,785 *Q. stellata*, 846 *Q. marilandica*, 2 *Celtis occidentalis*, 1 *Fraxinus pensilvanica* and 2 *Prunus americana*. For saplings, I mapped 54 *Q. stellata* and 21 *Q. marilandica*. The size class distribution of the two dominant species did not differ. The dominant mortality class was "standing dead", while I only found saplings less than 2 m tall. The spatial distribution of the species indicated segregation in the use of the environment, generating a clumped univariate distribution of stems of the same species within radii of 30 m, but repulsion outside 30 m. This segregation can be explained by the different ecological requirements of each species.

Keywords: conservation, point pattern analysis, *Quercus stellata*, *Q. marilandica*, size class distribution

Introduction

Cross timbers forests, such as those at the Tallgrass Prairie Preserve (TGP) in northeastern Oklahoma, are a mosaic of upland deciduous forests and savannas, occurring throughout southeast Kansas, eastern Oklahoma, and north-central Texas. Cross timbers, in general, have been defined as a mosaic of grasslands, savannah-like woodlands, oak thickets and forests (Dyksterhuis 1948; Rice and Penfound 1959; Risser and Rice 1971; Johnson and Risser 1972; Penfound 1962; Smeins 1994). These upland forests are primarily associated with sandstone derived soils and are dominated by *Quercus stellata* and *Quercus marilandica*, which occur in basins and on dry sites in tallgrass prairies (Bruner 1931; Rice and Penfound 1959; Rice 1965; Kroh and Nisbet 1983). The extent of dense cross timber forests and savannas is changing as a result of on-site management practices, with important area reductions in some locations and increases in others (Wethintong 1994).

Cross timbers play an important role in the natural history of this region. Francaviglia (2000) listed several reasons, suggested by regional planners, for preserving these forests, including the following: environmental diversity (because the forest environment differs from the surrounding prairie); habitat variety (the forests provide shelter and nesting sites for a variety of bird species); wildlife (the forests provide food for a diverse population of birds, mammals and reptiles); water conservation (they protect water-bearing sandstone from rapid runoff and erosion) and human recreation. Few efforts, though, have been made to evaluate the conservation status or study the ecology of these forests (Hoagland et al. 1999). Over the last decade several studies have offered new and useful information for conservation, such as the impact of tornados on forest structure (Shirakura et al. 2006), natural regeneration (Clark and Hallgren 2003), and spatial distribution (Arévalo 2002).

In this study I analysed the spatial distribution of stems and forest structure in a 4-ha cross timbers stand in the Tallgrass Prairie Preserve. Spatial patterns of trees are important characteristics of plant communities (Vacek and Lepš 1996). These patterns can reveal aspects of canopy replacement (Horn 1975; Woods 1979; Busing 1996), regeneration (Condit et al. 1992; Norton 1991) and changes in forest dynamics under disturbance (Alekseev and Zherebtsov 1995; Vacek and Lepš 1996), including spatial relationships between tree species (Hatton 1989; Collins and Khlar 1991; Duncan 1991; He et al. 1997). Moreover, the spatial distribution of trees can be an important factor to take into account when making management decisions about natural areas (Moeur 1993). The main hypothesis I tested in this study is that the dominant tree species (*Q. stellata* and *Q. marilandica*) have different environmental preferences

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and requirements, which is reflected in their spatial distributions. It has been demonstrated that spatial distribution patterns of species are often associated with environmental variation (Becker et al. 1988; Clark et al. 1998). No prior studies in the cross timbers region have investigated forest patterns and dynamics using a large mapped stand. Consequently, this study offers a unique opportunity to investigate spatial relationships between cross timber tree species and the environment.

Material and methods

Study site

The study was conducted in the bison unit of the Tallgrass Prairie Preserve (TGP) in Osage County, Northeast Oklahoma (36°49'N, 96°23'W), USA. The preserve encompasses approximately 15,200 ha of natural area owned and managed by The Nature Conservancy (TNC).

Tallgrass Prairie contains a large number of plant species, particularly from the Asteraceae, Poaceae and Fabaceae (Little 1938). Around 80% of the tall grass prairie is dominated by C4 warm-season grasses which include big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), Indian grass (*Sorghastrum nutans* Nash) and switch grass (*Panicum virgatum* L.). Much of the remaining area is forested by the dominant species *Q. stellata* and *Q. marilandica*, which exhibit different spatial preferences in the forest patches (Arévalo 2002).

The TGP preserve is managed to restore a remnant of the tallgrass prairie landscape in Oklahoma (Hamilton 1996). Many studies on tallgrass prairies stress the importance of fire and bison grazing in determining species composition and structure (Tarr et al. 1980). Prescribed burns are conducted throughout the year, and include dormant spring burns (March-April), late growing-season burns (July-September), and dormant fall burns (October-November). Burns are prescribed according to the fuel load of the vegetation (Hamilton 1996).

Sampling design

I located a 200 ×200 m plot in one of the cross timbers forests of the TGP Preserve. This forest can be considered representative of cross timbers forest at the preserve that increased in density after fire control was implemented prior to creation of the preserve in 1989 and the ensuing regular fires. Previously, the recurrence rate of fires had been lower and more irregular (Allen and Palmer 2011). The last fire occurred in this stand four years before my sampling. The sampling plot was located to cover as much forest as possible

During September and November 1998 I mapped all stems over 1.5 m height (taking one of the plot corners as a reference point, and mapping all trees with respect to that point) using a Cartesian coordinate system. In the square plot, each stem had an *x* and a *y* value, depending on how far away it was from the reference point (the chosen plot corner). I classified trees as all stems over 2.5 cm DBH (diameter at breast height), and saplings as all stems over 1.5 m height but less than 2.5 cm DBH. Saplings were also categorized into classes based on height (class 1, less than 2 m; class 2, less than 3 m; etc.). This classification was used for all tree species in the plot. Although, referred to here as saplings, many were stump sprouts or suckers, which is a common form of reproduction in these species (Clark and Hallgren 2003). Excavation being infeasible, I made no attempt to differentiate between seed sprouts, stump sprouts, and suckers.

Dead trees were also mapped and classified as standing dead (the tree was dead but still standing), broken dead (dead trees broken at a main stem height of more than 2.5 m), fallen dead (dead and fallen) and bent dead (dead and bent tree).

In order to represent the density and DBH values for different diameter classes I used diameter size classes in increments of 5 cm, except trees less than 2.5 cm, which were grouped together, and trees greater than 40 cm, which were also grouped together. It is common for the smaller size classes to have a shorter range class because of the high density of younger stems.

Statistical analysis

I correlated the densities (individuals/ha) of the stems of each size class for both species in the plots to determine the relationship between the size class distribution of both species in each plot (using Pearson correlation coefficients, for $p<0.05$ and n=7 size classes).

I studied the spatial distributions of *Q. stellata* and *Q. marilandica* in the plot using Ripley's univariate $K_1(t)$. With this analysis I determined if the spatial pattern of trees in the plot was significantly clumped or more evenly distributed than could be expected from a random spatial distribution. Since tree spatial pattern varies by successional stage, this helped to determine the successional status of the stand.

This function determines the consistency of the empirical distribution of distances among stems with Poisson expectations (Szwagrzyk 1992), and is given by the equation:

$$K_1(t) = \frac{v(A)}{n^2} \sum_{x \in A} \sum_{y \in A \cup B} 1_{(0,t]}(d(x,y)) \qquad (1)$$

In this analysis, the plot was divided into an inner circle (A) and a buffer zone (B), where: n = number of individuals per plot; $v(A)$ = area of the inner circle analyzed; t = distance between individuals; x,y = points of the Euclidean distance of the points x and y.

The buffer zones were included to address the potential problem of edge effects (Ripley 1977). To detect departure from complete spatial randomness (CSR), constant approximate confidence intervals were established by accepting the value ± 1.42 $(A/n-1)^{0.5}$ (where: A = area of the inner circle, and n = number of trees in the plot) as a reasonable approximation of the 5% significance points with 99 simulations (Ripley 1979).

I used the modified O-ring statistic provided by the software Programita (Weigand and Moloney 2004), which is similar to

Ripley´s K, but replaces the circles of radius r in the calculation with rings of radius r (Stoyan and Stoyan 1994). I selected this method because it offers some improvements in cases with irregular distribution of the points with respect to Ripley´s *K* (Weigand and Moloney 2004).

To analyze the spatial relationship between two species I used the K_{12} function for bivariate processes:

$$K_{12} = \frac{v(A)}{n_1 n_2}\sum_{x}\sum_{y} 1(0,t)d(x,y) \tag{2}$$

where n_1 and n_2 are the number of objects of a first and second type, x is the object of the first type and y is the object of the second type. The remaining symbols are as per the function K_1. Basic statistical methods followed Zar (1984) and were implemented using the SPSS statistical package (Anon. 1986).

Results

I mapped a total of 7,636 stems, including *Q. stellata* (6,785 stems), *Q. marilandica* (846), *Celtis occidentalis* (2), *Fraxinus pennsylvanica* (1) and *Prunus americana* (2) species. I mapped 75 saplings, all of which were *Q. stellata* (54) and *Q. marilandica* (21). I also mapped a total of 918 dead *Q. stellata* (770) and *Q. marilandica* (148) trees.

The size distribution of the stems of both species followed similar patterns in terms of density and basal area (Fig. 1). Density values (r=0.969, n=7; p<0.001) and basal area values (r=0.808, n=7; p<0.001) were significantly correlated, indicating that the size class distribution did not differ between the two species.

I only found saplings of class 1 and 2 for both species, with class 1 saplings dominant for both species, indicating a high degree of mortality at early ages (Fig. 2a.) With respect to types of mortality, dead trees of both species were dominated by standing dead (more than 70% of dead trees for both species), followed by broken dead (less than 20% for both species). Very low values were recorded for other classes of mortality (fallen dead and bent dead) (Fig. 2b).

The univariate spatial analysis revealed significant clumping for both dominant species (*Quercus stellata* and *Q. marilandica*) at distances up to 50 m (line of the function above the 95% interval of confidence). This spatial distribution was most intense within radii of 20 m around the trees (taking into consideration the buffer zone). Above 20 m, the clumping pattern was still significant, but gradually decreased in intensity at greater distances. The two species showed a similar pattern in their univariate spatial distributions (Fig. 3 a,b).

The spatial relationship between the two dominant species (*Quercus stellata* and *Q. marilandica*) using the bivariate O-ring statistic showed a significant repulsion between the two species within 30 m (using a 95% confidence interval; again, the further away from the interval they were, the more intense the rejection). After 30 m, spatial distribution between the two became random (Fig. 3c).

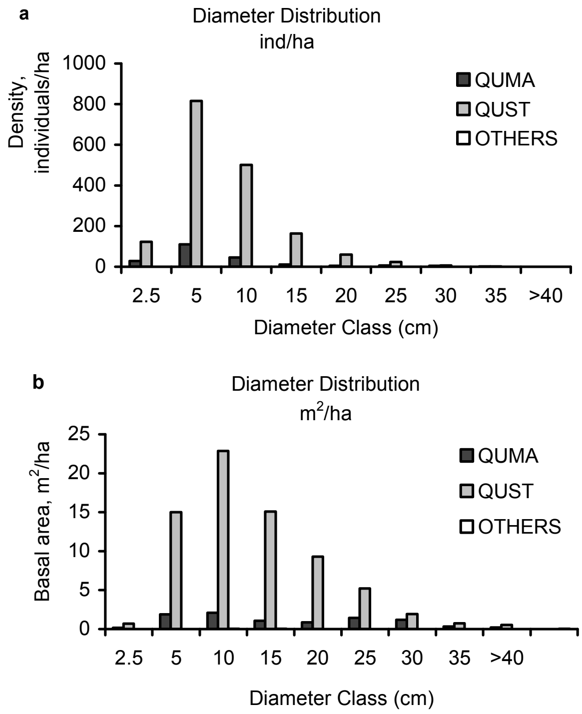

Fig. 1 Size class distribution based on (a) density (trees/ha) and (b) basal area (m^2/ha). Class 2.5 includes stems 2.5 cm diameter to 5 cm; class 5 includes stems 5 cm diameter to 10 cm, and so on.

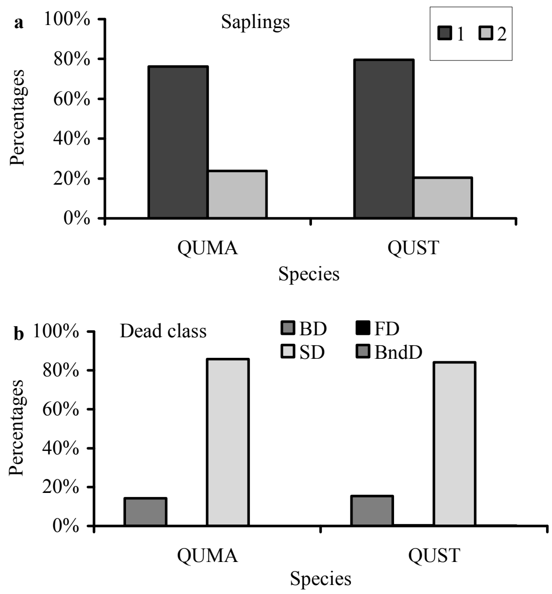

Fig. 2 (a) Percentage of saplings of class 1 (less than 2 m high) and class 2 (less than 3 m high). No saplings taller than that 3 m were found. (b) Percentage of individuals in the different classes of dead trees: BD= Broken dead trees, FD= Fallen dead trees, SD= Standing dead trees and BndD= Bend dead trees.

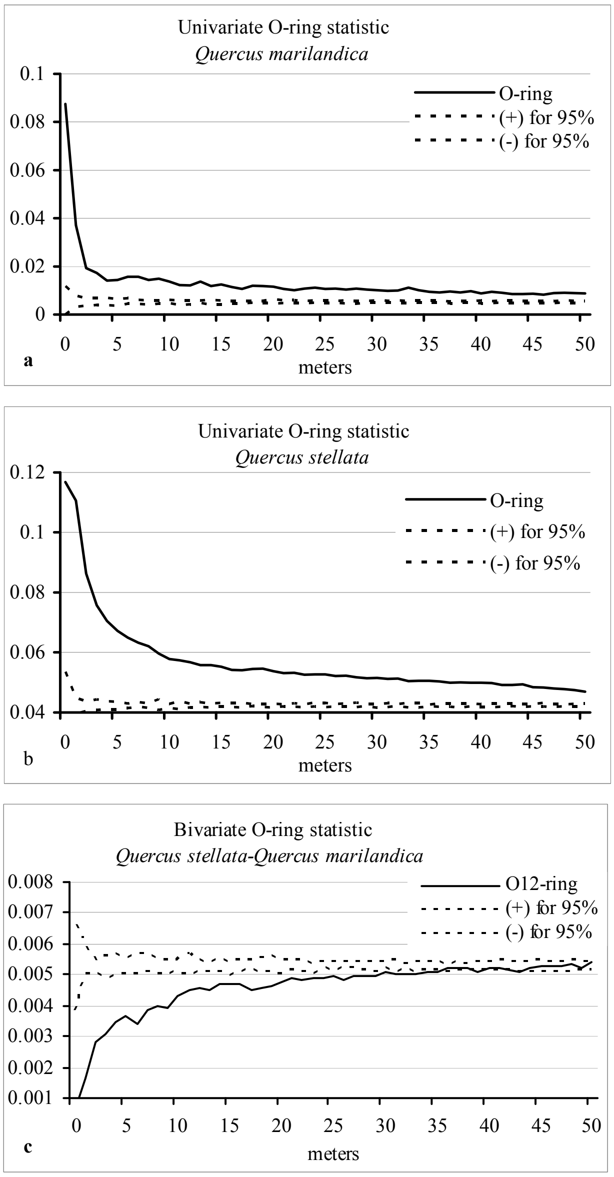

Fig. 3 Values of the O-ring statistic indicated in the Y-axis for (a) ***Quercus stellata*** **and (b)** ***Quercus marilandica.*** Dashed lines indicate 95% confidence intervals for a random spatial distribution while the full lines are the values of the statistic. Values over the line indicate significant spatial clumping, and values under the line represent spatial rejection. Distances for the calculations of spatial distribution are indicated in meters along the ordinate. (c) The bivariate O-ring statistic for both species.

Discussion

Results from structure and spatial distribution revealed that the two dominant species coexisted with differences in these aspects. Another study demonstrated spatial segregation (Arévalo 2002), leading to speculation on different habitat preferences. As is common in cross timbers forests of Oklahoma, *Q. stellata* was the dominant species (Kroh and Nisbet 1983).

I did not detect differences in size-class distribution between the dominant species (these values were positively correlated), suggesting similar size structure for the two species. Intense fires have been more common since the creation of the preserve (Hammilton, pers. comm.) and have affected the size structure of both species in a similar manner (Figure 1). Also types of mortality follow a similar pattern among both species, indicating a similar response to disturbances. These results are consistent with previous studies in other cross timbers forests (Rice and Penfoud 1959; Clark and Hallgren 2003).

The proportion of *Q. marilandica* saplings with respect *Q. stellata* (28 %) is higher than the proportion of *Q. marilandica* vs. *Q. stellata* trees (11 %). Fire may have a differential effect on the regeneration of the two species. In the case of *Q. douglassi*, fire favours regeneration (Mensing, 1990; Swiecki and Bernhardt, 2001). Fire, though, may be only one of many factors affecting regeneration. *Q. douglassi* regeneration may also be affected by humidity, predation, depth, slope, aspect, angle and canopy cover (Borchert et al. 1989). These factors may interact, producing results different from a single factor acting alone. *Q. douglassi* is very sensitive to grazing after fire which results in low recruitment (Arévalo et al. 2009).

Sapling mortality was very high, which is common in these species (Clark and Hallgren 2003). This was evident when comparing saplings of class 1 to saplings of class 2, the latter accounting for less than 20% of the total saplings, and the lack of detection of individuals over class 3 (indicating a low replacement rate).

The spatial univariate distribution of the species revealed aggregation over long distances (the line of the function is above the 95% confidence interval), but clumping was most intense in the first 15 m, indicating agregation patches of tha size of diameter approximately.

The spatial segregation revealed by the bivariate spatial analysis confirms previous results (Arévalo 2002) for these species and their differences in habitat distribution (Fig. 3c). *Q. stellata* and *Q. marilandica* commonly co-occur in the same habitats (Russell and Honkala 1990). However, there are some differences in the ecology of the species that may explain their distributional differences. For example, *Q. marilandica* tends to occur in more moisture-stressed conditions (Arévalo 2002), such as forest edges (Matlack 1993), than *Q. stellata* (Russell and Honkala 1990). *Quercus marilandica* tends to be shorter lived than *Q. stellata* (Miller and Lamb 1984) which can survive more than 400 years (Therrel and Stahle 1998). Species with shorter generation times, such as *Q. marilandica*, may be more suitable in transient conditions because they have mechanisms to respond to changing environments (Oliver and Larson 1990). Cross timbers forests at TGP are dynamic, and the area they cover has contracted over the last 40 years by approximately 25% (Wethington 1994). This could explain the lack of advanced regeneration found for both species in the study area. Again, this segregation is more intense in the first 10–15 m (line below the confident 95% confident interval).

Cross timbers forests face an increased risk of destruction from various human threats (Therrell and Stahle 1998). The

conservation of these forests (old-growth as well as young, recovered patches) will require continued research and conservation efforts in order to preserve these unique and important ecosystems.

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